

Feast not famine: Nitrogen pools recover rapidly in 25-yr-old postfire lodgepole pine

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Abstract. The extent of young postfire conifer forests is growing throughout western North America as the frequency and size of high-severity fires increase, making it important to understand ecosystem structure and function in early seral forests. Understanding nitrogen (N) dynamics during postfire stand development is especially important because northern conifers are often N limited. We resampled lodgepole pine (*Pinus contorta* var. *latifolia*) stands that regenerated naturally after the 1988 fires in Yellowstone National Park (Wyoming, USA) to ask (1) How have N pools and fluxes changed over a decade (15 to 25 yr postfire) of very rapid forest growth? (2) At postfire year 25, how do N pools and fluxes vary with lodgepole pine density and productivity? Lodgepole pine foliage, litter (annual litterfall, forest-floor litter), and mineral soils were sampled in 14 plots (0.25 ha) that varied in postfire lodgepole pine density (1,500 to 344,000 stems/ha) and aboveground net primary production (ANPP; 1.4 to 16.1 Mg·ha⁻¹·yr⁻¹). Counter to expectation, foliar N concentrations in lodgepole pine current-year and composite needles (1.33 and 1.11% N, respectively) had not changed over time. Further, all measured ecosystem N pools increased substantially: foliar N increased to 89 kg N/ha (+93%), O-horizon N increased to 39 kg N/ha (+38%), and mineral soil percent total N (0–15 cm) increased to 0.08% (+33%). Inorganic N availability also increased to 0.69 µg N-[g resin]⁻¹·d⁻¹ (+165%). Thus, soil N did not decline as live biomass N pools increased. Among stands, biomass N pools at postfire year 25 remained strongly influenced by early postfire tree density: foliar and litterfall N concentrations declined with lodgepole pine density and ANPP, but the foliar N pool increased. Lodgepole pine ANPP correlated negatively with annual resin-sorbed N, and we found no indication of widespread N limitation. The large increases in N pools cannot be explained by atmospheric N deposition or presence of known N fixers. These results suggest an unmeasured N source and are consistent with recent reports of N fixation in young lodgepole pine.

Key words: conifer; disturbance; ecosystem function; fire ecology; *Pinus contorta*; Rocky Mountains; stable isotopes; stand development; subalpine forest; succession.

INTRODUCTION

As the number and extent of high-severity fires have increased across western North America (Abatzoglou and Williams 2016, Westerling 2016), the area occupied by young postfire conifer forests has also grown. Over 1.15 million hectares of forest burned as stand-replacing fire between 1984 and 2010 in the U.S. Northern Rocky Mountains (~5% of total forested area), and the proportion of stand-replacing fire within individual fires increased from 22% to 27% (Harvey et al. 2016). These trends are projected to continue (Westerling et al. 2011,

Barbero et al. 2015), so understanding the structure and function of young postfire forests is necessary to anticipate the future of western forest landscapes (Swanson et al. 2011, Donato et al. 2012). Understanding nitrogen (N) dynamics in postfire stands is especially important because northern conifer forests are often N limited (Yang 1998, Kishchuk et al. 2002, Höglberg et al. 2017). Although N cycling following low-severity fire has been well studied (Wan et al. 2001, Hart et al. 2005), surprisingly few studies had focused on N following natural stand-replacing forest fires prior to the recent uptick in fire activity (Smithwick et al. 2005, Koyama et al. 2010). Further, knowledge of how N pools and fluxes vary over time and space as aggrading stands approach peak productivity during the decades after stand-replacing fire remains limited.

Fires initially reduce forest ecosystem N stocks because N is oxidized as biomass combusts (Maynard

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et al. 2014). In forests adapted to crown fires, N losses are driven primarily by combustion of live vegetation, because coarse wood consumption is low (e.g., ~8%; Tinker and Knight 2000), and fire effects typically do not extend into the mineral soil (Turner et al. 1999, Smithwick et al. 2009, Maynard et al. 2014). Nitrogen losses to fire may not be large because live biomass accounts for <15% of total ecosystem N (Page-Dumroese and Jurgensen 2006, Smithwick et al. 2009, Johnson and Turner 2014). In N-poor subalpine forests, remaining postfire N is highly conserved for up to 15 yr after crown fire because soil microbes immobilize N (Turner et al. 2007, Metzger et al. 2008, Högberg et al. 2017), even as rapidly growing young trees become a strong N sink (Turner et al. 2009). Plant demand for N may not exceed supply until tree biomass and nutrient demand increase substantially, and this “fire fertilization effect” may last up to 25 yr (Harden et al. 2003). Nitrogen pools and fluxes continue to change with time since fire as stands develop and plant demand for N increases (Hart et al. 2005). Recovery of carbon (C) stocks is driven by live vegetation growth and occurs within ~100 yr (Bradford et al. 2008, Kashian et al. 2013). Recovery of N stocks occurs within ~40–70 yr (Smithwick et al. 2009), but how N pools and fluxes vary over time and space is relatively unexplored (Litton et al. 2003a, Turner 2010). Under historical fire regimes (Turner and Romme 1994), there is no net depletion of N and C over multiple fire cycles, although N availability may decline as postfire stands reach peak productivity (Dunnette et al. 2014).

How young stands maintain high productivity for decades following fire has remained puzzling in N-poor forests that lack species known to fix N. Dense but spatially variable postfire tree regeneration is a hallmark of subalpine forests (Turner et al. 1997, 1999, Donato et al. 2016). Postfire stem densities often greatly exceed prefire densities if serotinous species such as lodgepole pine (*Pinus contorta* var. *latifolia*) are common (Turner et al. 1997, 2004, Franzese and Raffaele 2017). Young lodgepole pines grow rapidly and reach maximum rates of aboveground net primary production (ANPP) and fine root production between 24 and 60 yr of age (Pearson et al. 1987, Ryan et al. 1997, Olsson et al. 1998, Kashian et al. 2013, Schoonmaker et al. 2016). Dense stands subsequently self-thin as intraspecific competition intensifies during the fire-free interval (Kashian et al. 2005, Treurnicht et al. 2016), but evidence for N limitation in lodgepole pine is inconsistent (Fahey et al. 1985, Prescott et al. 1992, Binkley et al. 1995, Brockley 2003, Blevins et al. 2005, Turner et al. 2009). Symbioses with ectomycorrhizal fungi (EMF) may help young conifers during periods of rapid growth by facilitating nutrient transfer from soils to trees (Bothwell et al. 2001). Fungal biomass declines sharply following high-severity fire (Neary et al. 1999, Treseder et al. 2004, Holden et al. 2013), but persistence of EMF spores allows rapid colonization of postfire tree seedlings (Miller et al. 1998).

However, whether and when N begins to limit productivity is not well understood.

We extended long-term studies of N dynamics in naturally regenerated postfire lodgepole pine stands and asked (1) How have N pools and fluxes changed over a decade (15 to 25 yr postfire) of very rapid forest growth? (2) At postfire year 25, how do N pools and fluxes vary with lodgepole pine density and productivity? In answering these questions, we evaluated specific expectations for variation in lodgepole pine foliage, litter, and soils (Table 1). Direct in situ measurement of N transformations over time and across space is often impossible (Binkley and Hart 1989, Högberg et al. 2017). However, indicators of soil nutrient supply (e.g., soil nutrient pools, fluxes, and isotopes) and organismal indicators of nutrient limitation (e.g., foliar nutrient concentrations, ratios and isotopes) can collectively provide insights into potential nutrient limitation (Sullivan et al. 2014). Our hypotheses assumed minimal N inputs to these stands because species known to fix N were absent or at very low abundance in our study sites, and atmospheric deposition is low in this region. However, symbiotic and non-symbiotic N fixation has been reported in some young pine stands (Wei and Kimmins 1998, Bormann et al. 2002, Reed et al. 2011, Chapman and Paul 2012), suggesting the potential for associative N fixation in these young postfire stands.

STUDY AREA AND METHODS

Study area

This study was conducted in Yellowstone National Park (YNP) during 2012–2013 in 25-yr-old postfire lodgepole pine forests that regenerated following stand-replacing fires in 1988 (Appendix S1: Fig. S1). The park encompasses ~9,000 km² in northwestern Wyoming, and most of YNP lies on a high-elevation (~2,100 to 2,700 m above sea level) volcanic plateau with relatively gentle topography. About 80% of YNP is dominated by lodgepole pine forest. The climate is characterized by cold, snowy winters and dry, mild summers. Thirty-year climate normals (1981–2010) at the Old Faithful weather station indicate mean January temperature of −9.8°C, mean July temperature of 14°C, and mean annual precipitation of 64.4 cm (Western Regional Climate Center; data available online).⁵ Climate conditions were not unusual during our study; mean January temperatures were −8.3° and −12.1°C in 2012 and 2013, respectively; mean July temperatures were 15.9° and 15.8°C; and annual precipitation was 68.1 and 51.1 cm.

In YNP, severe stand-replacing fire kills all trees, consumes the shallow litter layer and exposes mineral soil; postfire forests have essentially no duff (Turner et al. 1999). The 1988 fires were large and severe, yet plant reestablishment was rapid and abundant (Turner et al.

⁵ <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?wyoldf>

TABLE 1. Specific expectations associated with changes and variation in N cycling in 25-yr-old postfire lodgepole pine stands.

Response variable	Expected result (rationale)
<i>Question 1: Change over time (postfire years 15 to 25) in N cycling variables</i>	
Foliar and litterfall N	
N concentration	decrease (dilution effect as foliage biomass increases or intra-specific competition for N intensifies)
N pool	increase (increased foliage biomass will increase N pool as trees compete effectively with soil biota for N)
Forest floor litter (Oi horizon)	
N concentration	no change (N concentration associated with decomposition would remain similar)
N pool	increase (even if concentration did not change, increased litter mass would be expected to increase the litter N pool)
Mineral soil	
Total soil N (0–15 cm)	decrease (N would shift from soil to live biomass as strength of the lodgepole pine N sink increases and mycorrhizae transfer soil N to the pines; immobilization of N in developing litter layer should also depress soil N)
Inorganic N availability	increase (N availability increases with stand age; Smithwick et al. [2009])
<i>Question 2: Among-stand variation with increasing stem density and/or ANPP at postfire year 25</i>	
Foliar and litterfall N	
N concentration	negative (dilution effect or intraspecific competition in foliage, which would be similar in foliage litterfall)
N pool	positive (increased biomass would increase foliar and litter N pools)
Forest floor litter (Oi horizon)	
Litter N concentration	unrelated (decomposing litter would likely have similar N concentration, regardless of litter biomass)
Forest floor litter N pool	positive (productive, high-density stands produce more litter, which should produce a larger litter N pool)
Mineral soil	
Total soil N (0–15 cm)	negative (lodgepole pine N demand will be greater in more productive stands, leading to decline in soil N pool; decomposition will also shift N from soils to litter in more productive stands)
Inorganic N availability	positive (because greater N availability should be associated with greater productivity in an N-limited ecosystem)

1997, 1999, Romme et al. 2016). Postfire lodgepole pine densities ranged from zero to >500,000 stems/ha, and pools and fluxes of C and N in the postfire landscape were strongly related to tree density (Litton et al. 2003a, b, Turner et al. 2004, 2009, 2016, Schoennagel et al. 2008). Nitrogen did not appear to limit lodgepole pine productivity through postfire year 15 (Turner et al. 2009).

Our study was conducted in 14 plots (50 × 50 m) from among 72 plots in a broader long-term study of landscape variation in postfire tree density and ANPP (Turner et al. 2004, 2016; see Appendix S1: Fig. S1, S2). Foliar N and soil N availability were studied previously at 15 yr postfire (Turner et al. 2009), and we intended to resample the same 14 plots. However, access to four plots was prohibited during summer 2012 because of grizzly bear (*Ursus arctos horribilis*) activity, so we resampled 10 of the original 14 plots and substituted four comparable plots for the inaccessible plots. Each of these four had also been sampled at 17 yr postfire for soil and litter N. All plots were dominated by lodgepole pine before and after the 1988 fires and spanned the range of naturally regenerated lodgepole pine densities (Turner et al. 2016). Plots were between 2,000 and 2,500 m elevation, had minimal topographic relief, and were within 2 km of a road. Parent material consisted of Quaternary rhyolite bedrock and rhyolite-dominated glacial deposits; soils were shallow inceptisols, loamy-skeletal,

mixed superactive Lithic Haplocrypts (Hechtman soil series).

Field sampling

Stand structure was sampled during summer 2012 following our previous protocols (see Turner et al. 2004, 2016). Briefly, post-fire lodgepole pine density was recorded along three 50 × 2 m belt transects in each plot; at 5-m intervals along each transect, the basal diameter and height of a lodgepole pine ($n = 25$ per plot) was recorded, and percent vegetative cover by species was measured within a 0.25-m² square sampling frame. Aboveground biomass and net primary production were estimated using species-specific allometric equations developed from trees harvested in our study area in 1999 (Turner et al. 2004) and 2012 (Copenhaver and Tinker 2014), and then extrapolated to the stand using tree basal diameters and density (Turner et al. 2009, 2016). We recalculated 2003 biomass for one plot (Gibbon Falls) using the allometric equations developed in 2012 because the trees already had large basal diameters (up to 8 cm) by 2003, and the equations developed for small trees especially overestimate foliage biomass for larger trees (Copenhaver and Tinker 2014).

Soils and forest floor litter were sampled during summer 2012. Each plot was divided into four 25 × 25 m

quadrants. Three 900-cm² samples of the forest floor litter layer (Oi) were collected in each quadrant by cutting and removing 30 × 30 cm sections at distances of 2, 3, and 5 m from the quadrant centroid. Samples were composited by quadrant and dried at 60°C to constant mass. Mineral soil cores (5 cm diameter × 15 cm depth) were collected adjacent to each forest floor litter sample using a PVC core ($n = 12$ per plot); most (~83%) fine roots of lodgepole pine are in the upper 15 cm of the soil profile (Schoonmaker et al. 2016). Surface litter was removed, and mineral soils were kept cool, transported to the field laboratory, then homogenized and sieved (2 mm) the same day and air dried.

Resin bags ($n = 20$ per plot) were deployed at 10 cm depth during summer 2012 and incubated for one year as an index of plant-available inorganic N. Free resin bags are effective in remote settings and correlate well with more labor-intensive measurements of net N mineralization (Binkley et al. 1986, 1992). Resin bags were constructed using 20 g of mixed bed ion exchange resin (J. T. Baker #JT4631-1; Phillipsburg, NJ, USA) tied inside a piece of undyed nylon stocking material (Binkley et al. 1992). Five resin bags were deployed around the centroid of each quadrant, tethered with monofilament fishing line and retrieved in summer 2013.

Litter traps ($n = 25$ per plot) were also deployed during summer 2012. Black plastic 1020 greenhouse trays (28 cm width × 54 cm length × 6.2 cm depth secured to the ground with 15-cm landscape staples) were positioned along each transect at the same 5-m intervals where pines were measured but 2 m to the side. Traps were retrieved during summer 2013, and all litter was oven dried. Lodgepole pine needles were separated from other litter, dry mass was recorded, and subsamples were reserved for chemical analysis.

For analysis of lodgepole pine foliar chemistry, we harvested two branches from the upper third of each of nine lodgepole pines (individuals nearest to the 5, 25, and 45-m litter-trap positions along each transect) during summer 2013. From one branch, we removed only fully expanded current-year needles; from the other branch, we removed all needles (hereafter, composite needles). Foliage was oven dried to constant mass at 60°C.

Laboratory analyses

General soil characteristics.—Soil cores were composited by plot for analysis of pH, soil organic matter (SOM), total N, P, K, Ca, Mg, and B at the University of Wisconsin-Madison Soil and Plant Analysis Lab in Madison, Wisconsin. We determined soil texture using the soil particle size hydrometer method (Elliott et al. 1999).

Nitrogen availability.—Resin bags were rinsed in deionized (DI) water and air dried, then extracted in 100 mL of 1 mol/L KCl and agitated for 1 h on a shaker table. For occasional damaged resin bags, we emptied the resin into a filter funnel, rinsed with DI water, and dried to

constant mass at 40°C prior to extraction (as above) so that N values could be normalized to the initial resin mass. Duplicate 10-mL aliquots of the extracts were filtered into 15-mL falcon tubes using a 25-mm glass fiber syringe filter and frozen. Extracts were analyzed for ammonium and nitrate N on an Astoria 2 segmented flow analyzer (Astoria-Pacific, Clackamas, Oregon, USA) following manufacturer's protocols. Resin-sorbed N was reported as the rate of N accumulation ($\mu\text{g N} \cdot [\text{g resin}]^{-1} \cdot \text{d}^{-1}$).

Foliage and litter mass and chemistry.—Forest floor litter samples for each plot were combined by quadrant, and composite needles and annual litterfall were combined by transect. Current-year needles were combined by plot to provide sufficient sample for analysis. Subsamples were ground to a fine powder using a Wiley mill and #40 screen. Total carbon and nitrogen concentrations in litter and foliage were determined by flash combustion on a Flash 2000 elemental analyzer (Thermo Fisher Scientific, Waltham, Massachusetts, USA) at UW-Madison.

Stable isotopes.—Natural abundance of ¹⁵N can be a useful indicator of N cycling (Hobbie et al. 2005, Hobbie and Högberg 2012, LeDuc et al. 2013, Sullivan et al. 2014), so we analyzed $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in current-year foliage, forest floor litter, and mineral soil samples. Pine foliage is typically depleted in ¹⁵N relative to soils, because ectomycorrhizal fungi pass light N to the plants (Kohzu et al. 2000, Hobbie et al. 2005, Hobbie and Högberg 2012, Craine et al. 2015). Mineral soil is typically enriched in ¹⁵N, with greater values in deeper soils (Craine et al. 2015). Our soil samples were 0–15 cm, coinciding with the location of most fine roots (Schoonmaker et al. 2016), but differences among plots could potentially suggest whether soil N reflected products of mineralization or N fixation. Samples were composited by plot prior to analysis (5 g each quadrant) and ground to fine powder in a Wiley mill. Samples were weighed (one-third in duplicate) into tin capsules for analysis with a Costech 4010 elemental analyzer attached to a Thermo Finnigan DeltaPLUS SP or V Flow Isotope Ratio Mass Spectrometer at UW-Madison. Results are presented as per mil (parts per thousand; ‰) deviations, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, relative to the international standards of Vienna Pee Dee Belemnite for C and atmospheric N₂ for N, with calibrated internal laboratory samples. Average difference between duplicate samples was 1.4‰ for natural abundance of $\delta^{15}\text{N}$ and 0.1‰ for $\delta^{13}\text{C}$.

Nitrogen pool calculations.—Litter and litterfall N pools (kg/ha) for each plot were estimated by multiplying percent N by mass. The foliage N pool (kg/ha) was estimated from foliage biomass (Mg/ha, computed from allometric equations and stand density) and N concentration of the composite needles. For a conservative estimate of the total live postfire lodgepole pine N pool, we computed branch and bole biomass from allometric

equations developed from destructive harvest of 24-yr-old lodgepole pines in our study area (Copenhaver and Tinker 2014). We then used published N concentrations of 0.0035% for bole wood and 0.17% for branch wood (Fahey et al. 1985) to estimate those N pools. For belowground biomass, we used estimates from Litton et al. (2003b), who found coarse plus fine root biomass to be ~20% of total live lodgepole pine biomass in 12-yr-old lodgepole pine stands. Belowground net primary production as estimated by the ratio of total belowground carbon allocation (TBCA) to (TBCA + ANPP) is remarkably constant across extreme gradients of tree density and stand age (Litton et al. 2004). Thus, we multiplied total lodgepole pine aboveground biomass by 0.25 to estimate belowground biomass and multiplied by 0.3% N for roots in moderate-density young stands (Litton et al. 2004) to estimate the belowground N pool. Estimates were summed to obtain the total live lodgepole pine N pool. To approximate the mineral soil (0–15 cm) N pool, we assumed a bulk density of 1.0 kg/L (mean from 0–15 cm measurements in 17 plots of 12–35 yr old postfire lodgepole pine in YNP; Smithwick et al. 2009, Kashian et al. 2013); multiplied by percent N, and converted to kg/ha. We also conducted a sensitivity analysis to assess the potential influence of uncertainty in tree measurements and foliar N concentrations on N pools (see Appendix S2).

Statistical analysis.—All statistical analyses were performed at the plot level ($n = 14$), consistent with the prior study (Turner et al. 2009). We compared means for foliar, litter, and soil variables in postfire years 15 and 25 across all 14 stands, but tests for significant changes over time (Question 1) used pairwise t tests ($\alpha = 0.05$) only for stands sampled in both years ($n = 10$). Pairwise differences were tested for normality prior to analysis. We also tested for a relationship between the change in estimated ecosystem N pool and the change in lodgepole pine ANPP to see whether greater increases in productivity were associated with more N accumulation. To assess among-stand variation at postfire year 25 (Question 2), we tested for correlations (Pearson r , $\alpha = 0.05$) of foliar, litter, and soil variables with lodgepole pine stem density and ANPP using all 14 stands. We also explored potential relationships at postfire year 25 between resin-sorbed N and foliar and litter N concentration and aboveground N pools. Variables were tested for normality prior to analysis, and lodgepole pine stem density and aboveground ANPP were \log_{10} -transformed. All statistical analyses were performed in SAS version 9.4 (SAS Institute 2014).

RESULTS

Stand characteristics and general soils

Among the 14 stands, lodgepole pine stem density averaged 58,605 stems/ha at postfire year 24 (Table 2),

and neither the mean nor median (11,750 stems/ha) differed from postfire year 15. Stem densities at postfire year 24 ranged from 1,500 to 344,000 stems/ha, comparable to postfire year 15 (Turner et al. 2009). Lodgepole pine aboveground live biomass at postfire year 24 was more than double that measured at postfire year 15 (Table 2). Foliage and branch biomass had nearly doubled, and bole biomass increased three-fold (Table 2). Lodgepole pine ANPP increased by ~60% since postfire year 15 (Table 2), and remained strongly and positively correlated with postfire stem density (see Turner et al. 2016). Lodgepole pine accounted for 88% of total ANPP, with graminoids and forbs comprising the rest (Table 2); shrub cover (*Vaccinium scoparium*) was minimal. The only putative N fixer observed in the plots was *Lupinus argenteus*, which remained at very low abundance and ANPP (Table 2), accounting for <1% of total ANPP at postfire years 15 and 24, respectively.

Forest floor litter mass remained similar, but annual litterfall about doubled since postfire year 15 (Table 2). Most litterfall (85%) in postfire year 25 was lodgepole pine foliage, whereas most litterfall (65%) in postfire year 15 was small woody material. Annual litterfall increased with lodgepole pine ANPP ($r = 0.86$, $P < 0.0001$). Soils were acidic, with pH averaging 5.4 or 5.5, and organic matter concentration was low, averaging 3% (Table 2). Neither soil pH nor soil cation concentrations differed between sampling years (Table 2). Soil texture was dominated by sand and was classified as either loam or sandy loam.

Change over time (Question 1)

Foliar nitrogen.—Lodgepole pine foliar N concentrations did not differ between postfire years 15 and 25 (Table 2, Fig. 1a). Current year needles averaged 1.33% N, and composite needles (needles of all ages along a given branch) averaged 1.11%N (Table 2). Live N pools increased substantially. The lodgepole pine foliar N pool nearly doubled to an average of 89 kg N/ha (Table 2), and total foliar N increased in all but one plot (Fig. 1c). The average total live aboveground N pool also nearly doubled to 106 kg N/ha (Table 2, Fig. 1d).

Litter nitrogen.—Forest floor litter (Oi horizon) N concentration averaged 0.82%N, an increase of about 25% between postfire years 15 and 25, and litter C:N ratio averaged 62.5, a decrease of 15% (Table 2, Fig. 1b). Annual litterfall N concentration averaged 0.65%N at postfire year 25 (Table 2) but had not been measured previously. The forest floor litter N pool averaged 39.4 kg N/ha at postfire year 25 and did not differ from postfire year 15 (Table 1). The annual litterfall N pool averaged 4.7 kg N·ha⁻¹·yr⁻¹ (Table 1) at postfire year 25, comparable to ~5% of the foliar N pool.

Soil nitrogen.—Total surface (0–15 cm) mineral soil N averaged 0.08%N at postfire year 24, an increase of

TABLE 2. Stand structure, biomass, productivity, and indicators of ecosystem function for 14 young lodgepole pine stands studied at postfire year 15 (data from Turner et al. [2009]) and postfire year 25 (this study).

Variable	15 yr postfire	25 yr postfire
Stand characteristics		
Stand structure and aboveground biomass		
Lodgepole pine density (stems/ha)	84,333 (47,009)	58,605 (29,378)
Lodgepole pine total aboveground biomass (Mg/ha)	14.3 (6.6)	36.7 (5.9)
Foliage biomass (Mg/ha)	4.6 (1.6)	8.3 (1.3)
Branch biomass (Mg/ha)	2.8 (1.2)	5.4 (0.94)
Bole biomass (Mg/ha)	6.7 (4.3)	23.1 (3.8)
Annual aboveground net primary production (ANPP)		
Lodgepole pine ($\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)	4.5 (1.5)	7.4 (1.19)
Total understory ($\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)	1.33 (0.21)	1.03 (0.08)
Putative N_2 fixer (only <i>Lupinus argenteus</i>)	0.012 (0.005)	0.046 (0.016)
Litter mass and annual litterfall		
Forest floor litter mass (Mg/ha)	4.37† (0.62)	4.98 (0.89)
Total annual litterfall ($\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)	0.35 (0.22)	0.75 (0.08)
Lodgepole pine needle litterfall ($\text{Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)	0.12 (0.37)	0.65 (0.09)
Foliar and litter nitrogen concentration		
Foliar N		
Current-year needles		
Foliar N concentration (%)	1.38 (0.03)	1.33 (0.04)
C:N ratio	35.6 (1.68)	39.4 (1.31)
Foliar P concentration	not measured	0.19
N:P ratio	not measured	7.1 (0.13)
Composite needles		
Foliar N concentration (%)	1.08 (0.04)	1.11 (0.03)
C:N ratio	48.9 (1.81)	49.5 (1.22)
Foliar P concentration (%)	not measured	0.10 (0.004)
N:P ratio	not measured	11.2 (0.24)
N resorption efficiency (%)	not measured	41.5 (1.2)
Litter N		
Forest floor litter		
Litter N concentration (%)	0.66† (0.04)	0.82 (0.03)
Litter C:N ratio	73.8† (2.57)	62.5 (2.6)
Annual litterfall		
Litterfall N concentration (%)	not measured	0.65 (0.02)
Litterfall C:N ratio	not measured	84.2 (3.3)
Aboveground nitrogen pools		
Lodgepole pine aboveground N pool (kg N/ha)	55.1 (17.3)	106.3 (15.7)
Foliar N pool (kg N/ha)	46.0 (14.8)	89.0 (13.0)
Branch N pool (kg N/ha)	4.9 (2.1)	9.2 (1.6)
Bole N pool (kg N/ha)	2.4 (1.5)	8.1 (1.3)
Forest floor litter N pool (kg N/ha)	28.6† (4.88)	39.4 (6.47)
Annual litterfall N pool ($\text{kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)	not measured	4.7 (0.48)
Soil properties and N availability		
General soils (0–15 cm)		
Total N (%)	0.06 (0.01)	0.08 (0.007)
Total N (kg/ha)	857 (76)	1200 (111)
Soil C:N	29.9 (1.53)	22.1 (0.75)
Soil organic matter (SOM; %)	3.0 (0.25)	3.0 (0.26)
pH	5.4 (0.06)	5.5 (0.06)
Exchangeable P (ppm)	8.8 (1.2)	13.6 (0.9)
Exchangeable K (ppm)	115 (5)	120 (5)
Exchangeable Ca (ppm)	409 (49)	423 (46)
Exchangeable Mg (ppm)	65 (9)	69 (9)
Soil texture		
Percent sand	not measured	53.4 (2.8)
Percent silt	not measured	35.5 (2.5)
Percent clay	not measured	11.0 (0.55)

TABLE 2. (Continued)

Variable	15 yr postfire	25 yr postfire
Annual resin-sorbed N ($\mu\text{g N} \cdot [\text{g resin}]^{-1} \cdot \text{d}^{-1}$)		
Total inorganic N availability	0.18 [†] (0.04)	0.69 (0.17)
Ammonium	0.13 [†] (0.03)	0.22 (0.05)
Nitrate	0.05 [†] (0.002)	0.47 (0.12)

Notes: All stands regenerated following the 1988 Yellowstone Fires. Values are means with SE in parentheses. Boldface type indicates significant differences between years (paired *t* test, *n* = 10 plots, all *P* < 0.05).

[†]Prior sampling of forest floor litter mass, forest floor litter N, and resin-sorbed N occurred during postfire year 17 (2005), rather than at postfire year 15 (2003).

about 33% between postfire years 15 and 24 (Table 1, Fig. 1e). Annual resin-sorbed inorganic N averaged $0.69 \mu\text{g N} \cdot [\text{g resin}]^{-1} \cdot \text{d}^{-1}$, more than triple the rate measured at postfire year 17, and nitrate-N represented about one-half of the total (Table 1). Resin-sorbed N increased between years in all but two stands (Fig. 1f).

Total live biomass and soil N pools.—Including estimates for root N and assuming that litterfall N at postfire year 15 represented 5% of the foliar N pool, as at postfire year 25, we estimated the mean live lodgepole pine N pool at postfire years 15 and 25 at 66.5 and 138.5 kg N/ha, respectively. This a net increase of 72.2 kg N/ha, or $7.2 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. The estimated mean increase in the soil (0–15 cm) total N pool among plots was 343 kg N/ha, or $34.3 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. For stands sampled in both time periods, total ecosystem N increased substantially (Fig. 1g), and the increase in total ecosystem N at each plot was strongly correlated with the increase in ANPP (Fig. 1h).

Spatial (among-stand) variation (Question 2)

Foliar nitrogen.—Current-year needle foliar N and P concentrations declined with increasing lodgepole pine stem density and ANPP (Fig. 2a, b; Table 3). Current-year foliar N:P ratios averaged 7.1 (Table 2) and declined with stem density but were unrelated to ANPP. Composite needle foliar N and P concentrations also declined with stem density and ANPP, but N:P ratios were unrelated to either (Table 3). Resorption of foliar N averaged $41\% \pm 1.2\%$ and was unrelated to stem density and ANPP. Lodgepole pine foliar N, branch N, and total live aboveground N pools were unrelated to stem density but strongly positively correlated with ANPP (Table 3, Fig. 2c–d). Only the bole N pool also correlated with stem density (Table 3).

Litter nitrogen.—Annual litterfall N concentration declined with lodgepole pine stem density and ANPP, whereas the annual litterfall N pool was unrelated to stem density but positively correlated with ANPP (Table 3). Forest floor litter N concentration was unrelated to either stem density or ANPP, but the forest floor

litter N pool was positively correlated with both stem density and ANPP (Table 3).

Soil nitrogen.—Lodgepole pine stem density and ANPP were negatively correlated with annual soil resin-sorbed ammonium (Table 3, Fig. 3a) and unrelated to total surface soil N, resin-sorbed nitrate, and resin-sorbed total N (Table 3). Herbaceous ANPP correlated positively with resin-sorbed N (Fig. 3b). Composite needle foliar N and annual litterfall N concentrations correlated positively with annual resin-sorbed ammonium ($r = 0.63$, $P = 0.0166$; $r = 0.55$, $P = 0.04$, respectively). Current-year needle foliar N and forest floor litter N concentrations and all aboveground N pools were unrelated to annual resin-sorbed N (all $P > 0.05$).

Stable isotopes.—Values of $\delta^{15}\text{N}$ averaged -3.97‰ (range -5.49 to -2.58‰) for current year foliage, -4.76‰ (range -6.41 to -3.10‰) for forest floor litter, and 2.23‰ (range 1.17 – 3.55‰) for mineral soil. None of these $\delta^{15}\text{N}$ values were related to stem density or ANPP (all $P > 0.05$). However, current year foliar $\delta^{15}\text{N}$ correlated positively (i.e., less depleted) with greater foliar N (Fig. 4a) and forest floor litter N concentrations (Fig. 4b). Forest floor litter $\delta^{15}\text{N}$ also correlated positively with resin-sorbed ammonium N ($r = 0.62$, $P = 0.0188$). Soil $\delta^{15}\text{N}$ correlated negatively (i.e., less enriched) with soil total N, and $\delta^{15}\text{N}$ values approached one as soil total N increased (Fig. 4c).

DISCUSSION

This study revealed rapid recovery of N pools in lodgepole pine forests from 15 to 25 yr after high-severity fire. After only 25 yr, the live lodgepole pine N pool was nearly 80% of the average total live N across a 300-yr lodgepole pine chronosequence (175.7 kg N/ha ; Smithwick et al. 2009). Counter to our expectations, lodgepole pine foliar N concentrations had not declined since postfire year 15, and there was no compensatory decline in soil N as live biomass N pools increased. Rather, nearly all measured N pools increased substantially, despite a paucity of putative N-fixing species. We also documented a persistent influence of spatial

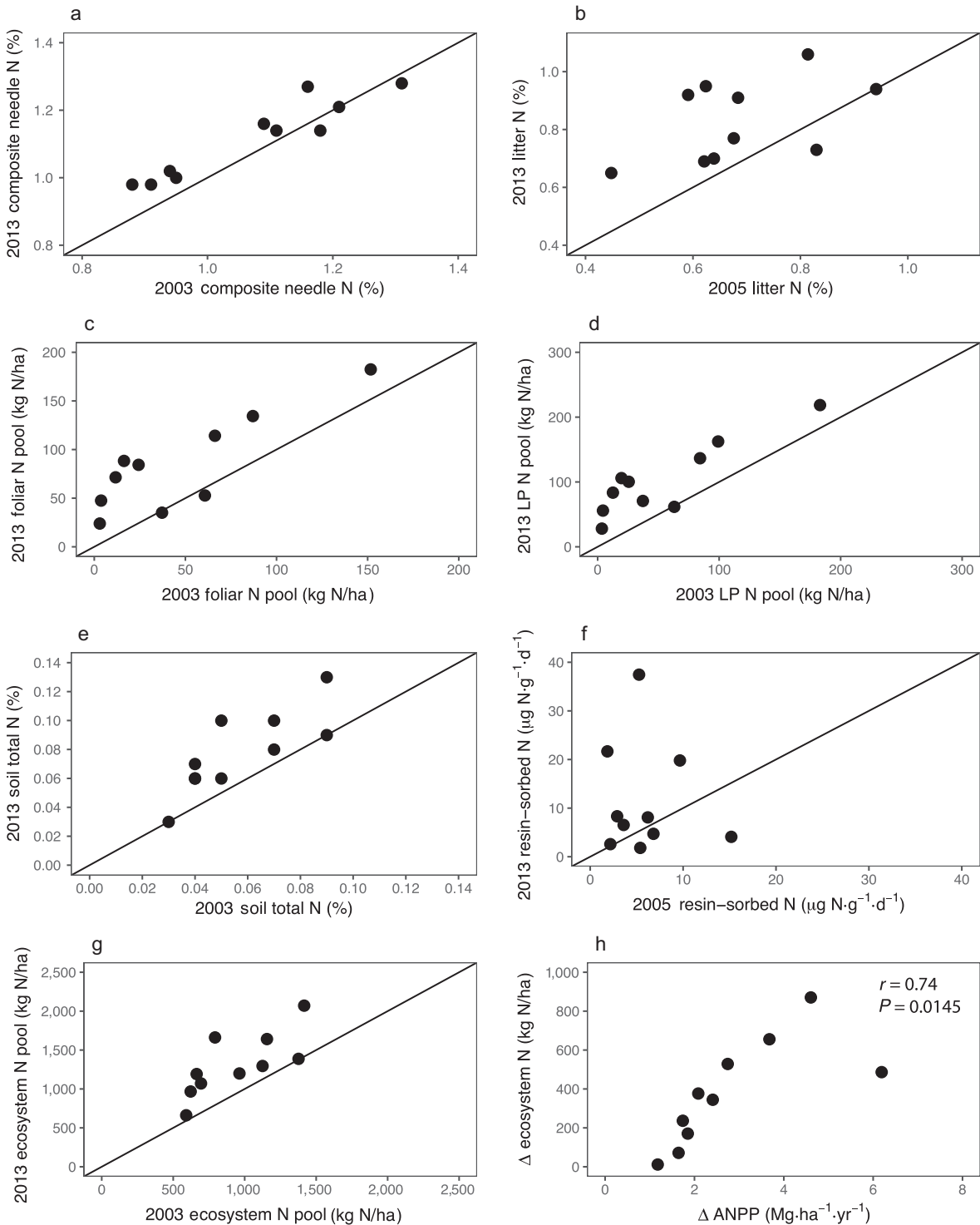


FIG. 1. (a) Lodgepole pine composite needle foliar N concentration, (b) forest floor litter N concentration, (c) lodgepole pine foliar N pool, (d) lodgepole pine total N pool, (e) total soil N, (f) resin-sorbed inorganic N, and total ecosystem N in postfire year 25 vs. postfire years 15 or 17 for stands in which measurements were made in both years ($n = 10$). Line indicates the 1:1 line (a–g). Panel h shows relationship between differences in total ecosystem N and annual lodgepole pine aboveground net primary production. Earlier data are from Turner et al. (2009).

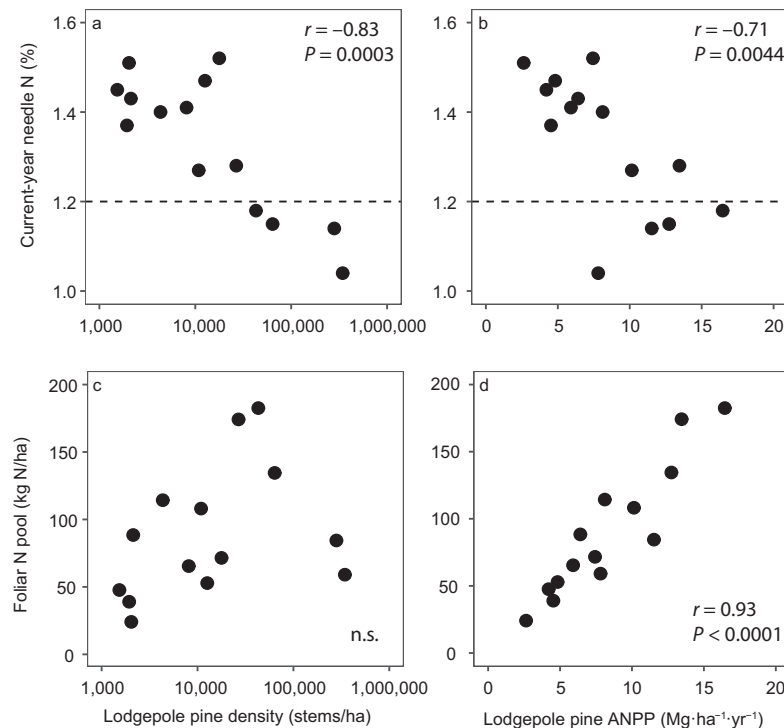


FIG. 2. Foliar N concentration in current-year lodgepole pine needles vs. (a) lodgepole pine stem density and (b) ANPP at post-fire year 25. Dashed line indicates the 1.2% N that can indicate N limitation. Foliar N pool vs. (c) lodgepole pine stem density and (d) ANPP at postfire year 25.

(among-stand) variation in postfire lodgepole pine regeneration on N dynamics; postfire trees are a strong N sink in rapidly growing forests (Hart et al. 2005), but the strength of that sink varies across the postfire landscape. We did not detect indicators of widespread N limitation at postfire year 25, and the potential sources of increased N are unresolved.

Change over time

Our expectations for change over time in foliar, litter, and soil N variables (Table 1) were only partly supported. The absence of a decline in lodgepole pine foliar N concentrations, despite the expected (and observed) large increases in live biomass N, indicates there was still sufficient N to sustain high productivity in 25-yr-old stands. Increased N was also reported in postfire stands of similar age in boreal forests of central Canada (Hume et al. 2016). A persistent fire-fertilization effect (Harden et al. 2003) is unlikely, given low N availability and substantial N immobilization up to 15 yr postfire (Turner et al. 2007, 2009, Metzger et al. 2008). However, our results are consistent with access to organic N via symbiotic EMF (Hobbie and Högborg 2012). Although direct assimilation of organic N is possible, the contrast between strongly negative foliar $\delta^{15}\text{N}$ and positive soil $\delta^{15}\text{N}$ values suggests that direct uptake is unlikely as a major source of tree N.

The increase in forest-floor litter N concentration likely indicates more foliar litter in the immobilization phase (Yavitt and Fahey 1986, Aber et al. 1990). Annual litterfall increased and shifted from woody to needle litter and was similar to litterfall amounts in 30-yr-old lodgepole pine stands (Olsson et al. 1998). Senesced lodgepole pine needles have lower N compared to green needles because N retranslocation efficiency is high (Prescott et al. 1989, Bothwell et al. 2001), but needle litter has more N and decomposes more readily than woody material (Rensburg and Turner 2006). Nitrogen content of fresh litterfall increases during initial phases of decomposition; e.g., lodgepole pine needles increased from 1.0%N to 1.3%N after two years of in situ incubation (Rensburg and Turner 2006). Nitrogen continues to accumulate in lodgepole pine needles for 6–7 yr following leaf fall, with 80% of the increased N derived from the soils below the litter layer (Fahey et al. 1985). Litterfall in aggrading stands should continue to increase Oi horizon N concentration as long as annual litterfall is increasing.

Resin-sorbed N increased over time and was similar to rates reported in other studies (Olsson et al. 1998, Smithwick et al. 2009, Griffin et al. 2013). However, increases in total soil N were surprising, as we expected mineral soil N (0–15 cm depth) to decline as N was sequestered by the rapidly growing trees (Chapman et al. 2005, Hart et al. 2005) and translocated to decomposing

TABLE 3. Pearson correlation coefficients for foliage, litter, and soil variables and postfire lodgepole pine stem density and ANPP in 25-yr-old postfire lodgepole pine stands ($n = 14$) in Yellowstone National Park.

Variable	Correlation coefficient (r)	
	Stem density†	ANPP†
Foliar and litter N concentration		
Current-year needles		
Foliar N concentration	−0.83***	−0.71**
Foliar C:N ratio	0.86***	0.67**
Foliar P concentration	−0.59*	−0.65**
Foliar N:P ratio	−0.61*	NS
Composite needles		
Foliar N concentration	−0.84***	−0.85***
Foliar C:N ratio	0.84***	0.86***
Foliar P concentration	−0.75**	−0.77**
Foliar N:P ratio	NS	NS
Litter		
Forest floor litter N concentration	NS	NS
Litterfall N concentration	−0.74**	−0.85***
Aboveground nitrogen pools		
Lodgepole pine aboveground N pool	NS	0.93***
Foliar N pool	NS	0.93***
Branch N pool	NS	0.76**
Bole N pool	0.70**	0.99***
Forest floor litter N pool	0.70**	0.58*
Annual litterfall N pool	NS	0.63*
Soils		
General soils		
Soil total N (%)	NS	NS
Soil organic matter (%)	NS	NS
Soil phosphorus (ppm)	NS	NS
Annual resin-sorbed N		
Nitrate-N	NS*	NS
Ammonium-N	−0.55*	−0.53*
Total inorganic N	NS	NS

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = not significant.

†Variable was transformed $\log_{10}(x + 1)$ prior to analysis.

litter (Fahey 1983). The increase in soil N may reflect increased soil microbial biomass, especially EMF, which can be a strong N sink (Högberg et al. 2017). EMF activity increases where inorganic N availability is low (Wallander et al. 2010), and trees may increase the relative allocation of belowground carbon to EMF in N-poor ecosystems (Högberg et al. 2017). Further, EMF mycelial biomass may peak during the period of most rapid tree growth, as observed in 10–30 yr old managed *Picea abies* stands (Wallander et al. 2010) and postfire boreal forest (Holden et al. 2013). Some increased soil N could have been translocated from deeper soils by fungal hyphae and plant roots (Johnson and Turner 2014). However, the 15-cm depth of our soil measurements coincides with where most root tips are found in Yellowstone (Byrd et al. 2000, Bothwell et al. 2001). Further, the decline in soil $\delta^{15}\text{N}$ with increasing soil N content

would be unexpected if highly processed older N was the main N contributor.

Spatial (among-stand) variation

Our expectations for variation in foliar and litter N were largely supported. Early postfire lodgepole pine densities continued to shape landscape patterns of nitrogen pools and fluxes through 25 yr and were similar to patterns observed at postfire year 15 (Turner et al. 2009). The decline in foliar N concentration with increasing tree density and ANPP is consistent with dilution effects that can occur with or without N limitation. Strong positive correlations between live lodgepole pine biomass N pools and ANPP (but not stem density) at 25 yr postfire support the suggestion that stands may converge in function before they converge in structure (Turner et al. 2016). However, the paucity of relationships most soil variables and tree density or ANPP was surprising. Dense, more productive stands produced more litter of lower N concentration, but this among-stand variation in litter quality appeared to have little influence on N flow from soils to trees (Högberg et al. 2017). Dense, productive stands with high litterfall (and high N demand) may stimulate EMF activity and circumvent negative effects of low-quality litter on N mineralization because EMF immobilize more N when their C supply is greater (Hasselquist et al. 2016). Further, resin-sorbed ammonium was lower in dense, productive stands, opposite to the expected relationship between N availability and productivity if inorganic N was limiting. In contrast, herbaceous ANPP increased with N availability, suggesting that lodgepole pine is likely reducing available N for understory vegetation.

The lack of relationship between lodgepole pine ANPP and soil total N may have several explanations. The abundance of organic N in the soils (60–75% of ecosystem N; Smithwick et al. 2009) supports N transfer to the trees via EMF or direct uptake (Nasholm et al. 2009, Inselsbacher and Näsholm 2012, Högberg et al. 2017), but makes a relationship between ANPP and soil total N unlikely. Further, EMF may sequester much N in their biomass and not transfer that N to their tree hosts (Nasholm et al. 2013, Högberg et al. 2017). The presence of N_2 -fixing organisms also could disrupt relationships between soil N and tree ANPP (Sullivan et al. 2014).

Using multiple lines of reasoning (sensu Sullivan et al. 2014), we found no evidence for widespread N limitation in these 25-yr-old postfire forests. Mean current-year needle foliar N remained above 1.2%, which can be indicative of N limitation (Binkley et al. 2000, Brockley 2003, 2007, Moore et al. 2004). Foliar N concentrations and pools were unrelated to N availability, in contrast to studies of N limitation in lodgepole pine saplings in British Columbia (Lilles et al. 2014). Foliar N:P ratios declined with stem density but were unrelated to ANPP, also suggesting N was not limiting productivity.

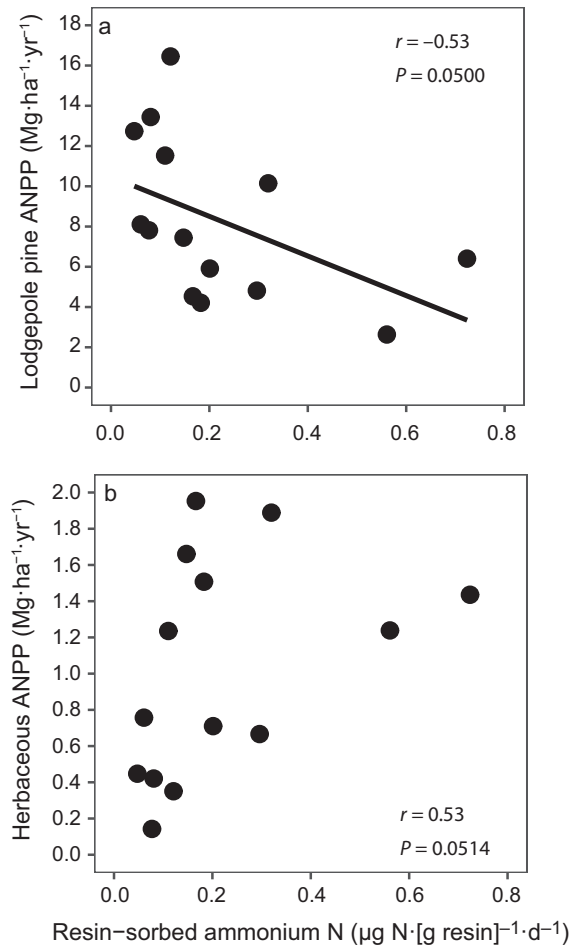


FIG. 3. Stand-level (a) lodgepole pine and (b) herbaceous aboveground net primary production vs. annual resin-sorbed ammonium N at postfire year 25. For panel b, Spearman's rank order correlation is shown.

Additionally, nearly all measured N pools increased over time. Thus, factors other than N likely limit lodgepole pine productivity at this stage of stand development. Prioritization of height growth by lodgepole pines (Claveau et al. 2002) suggests strong competition for light, and water availability also could play a role (Litton et al. 2003a).

Potential N sources

Collectively, our data raise a key question: where does the increased N come from? In mature N-limited forests, internal turnover of N is much larger than inputs or outputs, and rates and feedbacks (e.g., litter quality) within the local plant–soil ecosystem influence N cycling (Högberg et al. 2017). However, in aggrading postfire forests, the N lost during stand-replacing fires must be replenished. Ectomycorrhizal fungi transfer N from soil to trees to support productivity, and saprotrophic fungi transfer N from soils to litter during decomposition. However,

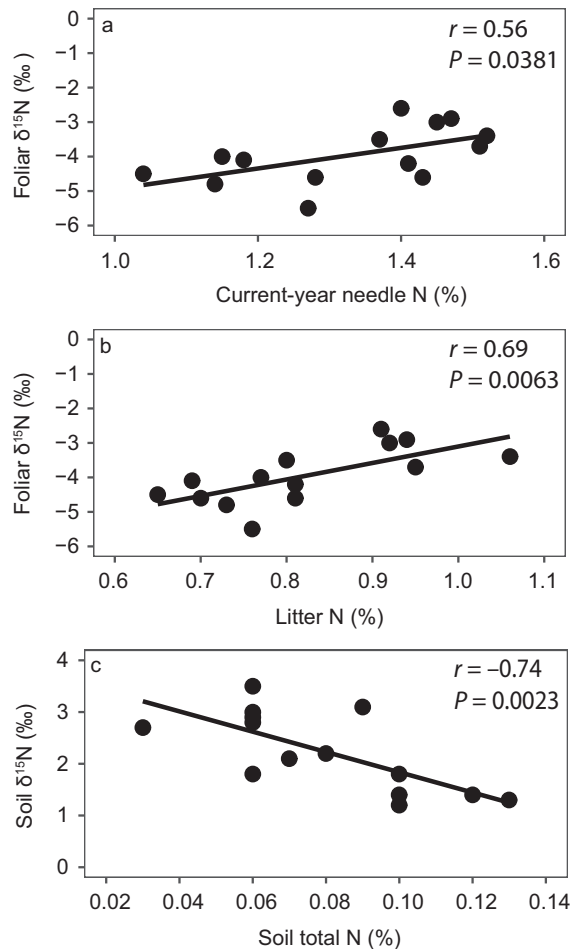


FIG. 4. Current-year lodgepole pine needle $\delta^{15}\text{N}$ vs. (a) current-year needle foliar N and (b) forest floor litter N and (c) soil $\delta^{15}\text{N}$ vs. soil total N, all at postfire-year 25.

neither alone can explain the postfire recovery of N reported here, and we briefly discuss potential sources.

Atmospheric N deposition is a possible source of N, but our conservative estimate of live lodgepole pine N accrual over 10 yr greatly exceeds atmospheric deposition in YNP during this time period, which is typically only 2–3 kg N·ha⁻¹·yr⁻¹ (National Atmospheric Deposition Program; data *available online*).⁶ Thus, N deposition is not sufficient even to meet live biomass N demand. Translocation of old N from deeper soils is also possible, but we think this is unlikely. Bulk soil $\delta^{15}\text{N}$ averages between 2‰ and 6‰ and generally increases with depth (Hobbie and Högberg 2012); if N from deeper soils was enriching the soils, we would expect a positive relationship between soil total N and soil $\delta^{15}\text{N}$, not the inverse relationship we observed.

Biological N fixation is another possible source. Post-fire N recovery in some forests is attributed to increased cover and productivity of N-fixing organisms (e.g.,

⁶ <http://nadp.slh.wisc.edu/data/>

lichens; free-living soil bacteria; or early successional plants with root nodule symbioses, such as *Alnus*, *Myrica*, *Lupinus*, and *Ceanothus*; Reed et al. 2011, Johnson et al. 2012, Maynard et al. 2014, Blasko et al. 2015). Following stand-replacing fires in California and Nevada, rates of N fixation of up to 40 to 70 kg N·ha⁻¹·yr⁻¹ could account for increased ecosystem N over 20 yr (Johnson et al. 2012). However, the lodgepole pine forests of Yellowstone have sparse cover of putative N-fixing species. Endophytic N-fixing bacteria have been reported in several conifer species (Bal et al. 2012, Carrell and Frank 2014, Moyes et al. 2016), but estimated N inputs (0.01–0.02 kg N·ha⁻¹·yr⁻¹) are low (Moyes et al. 2016). Non-symbiotic N fixation occurs in detrital downed wood, but primarily in advanced stages of decomposition (Fahey 1983, Jurgensen et al. 1987, Wei and Kimmins 1998) rather than in the sound logs abundant at our sites (Nelson et al. 2016). Further, measured rates of asymbiotic nitrogen fixation in woody debris suggest it could take 180 yr to replace N lost to wildfire (Wei and Kimmins 1998). However, our results indicate that stands with the greatest increases in lodgepole pine productivity also had the greatest increases in ecosystem N pools, suggesting a potential role of the young pines.

Several studies have suggested that N can accumulate in young pines in the absence of known symbiotic N fixers (Bormann et al. 2002, Chapman and Paul 2012), although sources of so-called “occult nitrogen” (Binkley et al. 2000) have proven challenging to find. “Mycorrhiza helper bacteria” associated with EMF root tips are increasingly reported across a range of hosts, and many taxa can potentially fix N (e.g., orders Burkholderiales and Rhizobiales; Nguyen and Bruns 2015). Symbiotic biological N fixation associated with tuberculate ectomycorrhizae in some young lodgepole pines appears to be sufficient to meet N demand (Paul et al. 2007, Chapman and Paul 2012). Nitrogen fixation in young lodgepole pines in British Columbia is associated with *Suillus tomentosus* (Paul et al. 2007, Chapman and Paul 2012), a long-range forager (Hobbie and Högborg 2012) that also occurs in YNP (Byrd et al. 2000, Douglas et al. 2005). Thus far, we have been unable to locate such tuberculate structures in our study sites, but soil crusts, including foliose lichens, seem to have become more conspicuous by 30 yr postfire (M. G. Turner and C. J. Cleveland, *personal observations*). We also were unable to distinguish ultimate sources of N because EMF and N-fixing bacteria both become enriched in ¹⁵N and send the lighter ¹⁴N to their hosts. However, an inverse relationship (as we observed) between soil δ¹⁵N and soil N content in an arid juniper woodland was indicative of N entering the ecosystem from N₂-fixing cyanobacteria and lichens in the soil crust (Evans and Ehleringer 1993). Better understanding of the intricate relationships between trees, EMF, microbes, and lichens across a wide range of conditions (stand age, stand structure, etc.) is needed to resolve these dynamics. As highlighted by Bormann et al. (2002), studies aimed at identifying ecologically important rates

and sources of N₂ fixation in N-poor systems lacking other obvious sources of N are needed.

In conclusion, we documented surprisingly rapid recovery of N stocks following the high-severity 1988 Yellowstone fires and a persistent legacy of postfire tree-regeneration patterns on N fluxes and pools. Rather than indicating widespread N limitation, our data suggest an unmeasured source of N (Johnson and Turner 2014). These results and other reports (Bormann et al. 2002, Chapman and Paul 2012, Craine et al. 2015, Moyes et al. 2016) underscore the need for long-term measurements of N cycling across stands of varying ages and structures (Prescott 2014), especially to identify cryptic sources of N (*sensu* Binkley et al. 2000). Such knowledge is increasingly important in western North America as more forests burn at high severity each year and the extent of young forests increases.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2626/supinfo>

DATA AVAILABILITY

Data are available from the EDI Data Portal: <https://doi.org/10.6073/pasta/3b2cc6cf9d2b4dd3a497b58119e234c>

Turner, M. G., T. G. Whitby, and W. H. Romme. Feast not famine: Nitrogen pools recover rapidly in 25-yr old postfire lodgepole pine. *Ecology*.

Appendix S1: Map and Photos of Study Plots

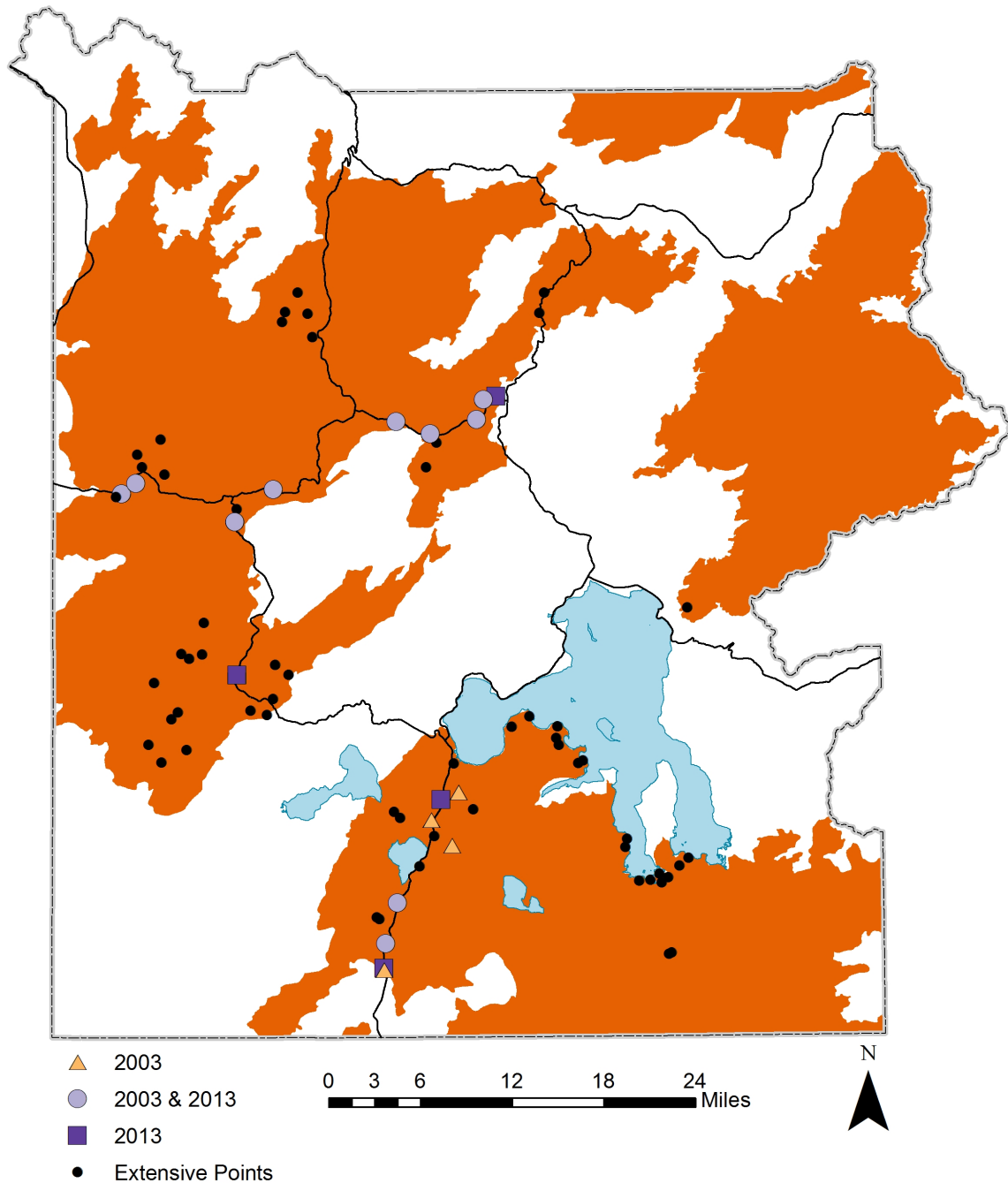


Figure S1. Distribution of study plots in Yellowstone National Park in which nitrogen dynamics were sampled at postfire-years 15 (2003) and 25 (2013) in stands of lodgepole pine that regenerated naturally from the 1988 Yellowstone Fires. Red shading depicts overall extent of the 1988 Yellowstone Fires. Major lakes and roads are also shown.

Postfire-yr 15



Postfire-yr 24



Figure S2. Photos from three of the re-sampled plots taken in 2003 (postfire-yr 15) and 2012 (postfire-yr 24). Lewis Canyon (upper), Riddle Hobo (center), Gravel Pit (lower).

Turner, M. G., T. G. Whitby, and W. H. Romme. Feast not famine: Nitrogen pools recover rapidly in 25-yr old postfire lodgepole pine. *Ecology*.

Appendix S2: Sensitivity Analysis

When constructing nutrient budgets for an ecosystem, there is uncertainty in estimates of concentration and mass that can propagate. However, relatively few studies in ecosystem ecology assess and report these uncertainties (Yanai et al. 2010, 2018). In this study, plots were selected along a gradient of postfire stem densities and rates of aboveground productivities, and empirical measurements in each plot were used to estimate stand-level N pools. In some cases, we cannot estimate uncertainties. For example, soils were composited by plot prior to analysis, so we have no estimates of variance. Also, soils were analyzed in different years (albeit at the same lab), and although standards are run, there could be differences in the lab.

To assess the sensitivity of N pool estimates to uncertainty in two key empirical measurements – basal diameter of measured trees, which is the predictor of tree biomass in the nonlinear allometric equations; and foliar N concentration, which was measured on multiple trees within each plot – we conducted a sensitivity analysis. We also examined within-plot coefficients of variation for insight into magnitudes of different sources of uncertainty.

Sensitivity of aboveground lodgepole pine N and total ecosystem N to biomass estimates and foliar N concentrations

Biomass. To obtain biomass components at the stand level (Mg/ha, as computed within Turner et al. 2016), calculations are done in SAS as follows.

- Basal diameter (cm) was measured on 25 trees/plot (nearest to the 5-m mark on the 3 transects); these are a random sample of 25 individuals in an even-aged cohort and based on testing of sampling different numbers of trees (in 1999), we found that this sample size yielded a reasonable estimate of tree size because tree diameters vary more among plots that vary in stem density than within plots.
- Allometric equations use basal diameter to predict biomass components on each of the 25 trees. Variable names refer to foliage biomass, aboveground biomass, bole biomass, branch biomass, and biomass is predicted in g/tree as follows:

```
treefolbio = 9.56*(basdiam**2.37);  
treebolebio = 47.75*(basdiam**2.05);  
treebranbio = 1.99*(basdiam**2.92);
```
- Along each of three 50-m x 2-m belt transects, we calculate the mean tree foliage, branch and bole biomass (g/tree) using the individual trees along each transect (n = 8, 9, 8)
- The mean tree biomass is multiplied by the density of trees on that transect and converted to standard units (Mg/ha);
- Biomass is then averaged across the 3 transects (Mg/ha) to obtain the plot estimate.

N pools. Foliage was sampled from 9 trees in each plot, and foliar N concentration was analyzed then averaged over the 9 trees. This concentration was multiplied by the foliage biomass to estimate foliar N pools. For branch and bole N pools, biomass was multiplied by N concentrations reported from the literature (so there is no within-plot variance).

Sensitivity analysis. To assess uncertainty, I re-computed aboveground lodgepole pine N pools and total ecosystem N pools on each plot for 2013 in three ways (Table S1):

1. Recompute aboveground lodgepole pine N pools and total ecosystem N pools using \pm 10% of the foliar N concentration measured within that plot (but keep biomass estimates as calculated initially for each plot);
2. Recompute aboveground lodgepole pine N pools and total ecosystem N pools using \pm 10% of the basal diameter measurements on each tree in the plot by recalculating biomass and then N pools (but keep foliar N concentration as the mean for each plot)
3. Recompute aboveground lodgepole pine N pools and total ecosystem N pools using the $-$ 10% of both foliar N and basal diameter on each plot and $+10\%$ of both foliar N and basal diameter on each plot. These estimates reflect a multiplicative effect of underestimating and overestimating the key N pools with based on 10% measurement error.

Because lodgepole pine biomass increased substantially during the 10 years, the conclusion of increased aboveground lodgepole pine N (Figure 1D) would still be supported. In addition, because lodgepole pine N makes up only a portion of total ecosystem N, our conclusions about increased total ecosystem N pools (Figure 1H) also would still be supported.

Coefficients of variation: Litter mass, litter N concentration, and foliar N concentration

Measurements of N concentration in lodgepole pine foliage (9 trees per plot) and forest floor litter (4 samples per plot) had relatively low variation within plots. Within-plot CV averaged 10.7% and 18.8% for foliar N concentration and forest floor litter N concentration, respectively. There was more variation in within-plot measurements of forest floor litter mass, however, with an average CV of 57.8%. This variation is real; we removed 30 cm x 30 cm sections of the forest floor, but positions underneath the tree canopy could have substantially more needle litter than locations that were not under the tree canopy. Furthermore, litter is continuously turning over as inputs and decomposition act in opposite direction. Our results did not show a significant change in the forest floor litter N pool (see Table 2), so incorporating measures of uncertainty would not alter this conclusion. However, this analysis points to the getting a more precise estimate of forest floor litter mass in future studies.

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Table S1. Plot-level results of sensitivity analysis based on foliar N concentration and basal diameter of sampled 24-yr-old lodgepole pine trees. Columns labeled “Original” are the estimate used in this study. Ranges in subsequent columns indicate results using -10% to +10% for foliar N concentration and measured basal diameter individually, then (-10% foliar N concentration and -10% basal diameter) to (+10% foliar N concentration and +10% basal diameter), which would reflect the largest error.

Site	2013 Aboveground Lodgepole Pine N (kg ha ⁻¹)				2013 Total Ecosystem N (kg ha ⁻¹)			
	± 10%				± 10%			
	Original	± 10% [N]	± 10% BD	[N] and BD	Original	± 10% [N]	± 10% BD	[N] and BD
84blowdown	137	125-148	106-172	97-186	1072	1060-1083	1041-1107	1032-1121
BiscBas	210	192-227	163-263	150-285	1150	1132-1166	1103-1203	1089-1224
CascCk	47	43-50	36-58	33-63	967	963-970	956-979	953-983
CascMeaN	56	51-61	43-71	40-76	968	964-973	956-983	952-989
CascMeaS	84	76-91	65-105	60-114	1663	1656-1670	1645-1684	1639-1693
CygLkNo	62	56-67	48-77	44-84	1296	1291-1301	1282-1312	1279-1319
FirLopSo	163	149-176	126-204	116-221	663	649-676	627-704	616-721
FounEast	100	92-109	79-126	72-136	1643	1634-1651	1621-1668	1614-1678
GibFalls	219	200-237	170-274	156-297	1200	1182-1218	1152-1256	1138-1279
GravPit	71	65-77	55-89	51-96	1192	1187-1198	1177-1210	1172-1218
LewCan	28	26-30	22-35	20-38	1388	1385-1390	1382-1396	1380-1399
PitchHOB	106	97-115	82-133	75-144	2072	2063-2080	2048-2099	2041-2110
RidLkHO	77	71-84	60-97	55-105	1619	1612-1625	1601-1638	1596-1646
SoLewCan	129	118-140	100-162	92-176	1946	1935-1956	1917-1979	1909-1992
MEAN	106	97-115	83-133	76-144	1346	1337-1355	1322-1373	1315-1384